Factors affecting zooplankton biodiversity in an arctic fjord: an analysis of three decades of data from Kandalaksha Bay, White Sea, Russia

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Abstract

The seasonal and intra-annual zooplankton community structure, biodiversity and abundance trends in Kandalaksha Bay, White Sea, were described and related to climate related and biological environmental variability over the period 1964 - 1998. 22 taxa, containing both holoplanktonic and meroplanktonic forms were studied. Seasonal variability of the White Sea zooplankton was characterized by overlapping peaks in abundance and biodiversity from the start of June to the start of October. A shift from predominately negative to positive zooplankton abundance and temperature anomalies, signifying an increase in total abundance and a warming of Kandalaksha Bay was observed from the mid eighties. The two most abundant species, *Oithona similis* and *Pseudocalanus minutus* showed opposite trends in relative abundance over the study period; *O. similis* decreased in relative abundance while *P. minutus* increased in relative abundance. There was also indication of long-term changes among other species: *Calanus glacialis* and *Sagitta elegans* increased, whereas relative abundance of *A. longiremis*, larval Bivalves, larval Echinoderms and *Oncea borealis* decreased. Yet, overall biodiversity, expressed by the Shannon index remained relatively stable during the years of study, and showed no clear signs of a long-term trend. All species had significant ($p < 0.01$) multiple regression models and the regressions analysis yielded high degree of explanatory value for the species *S. elegans, C. glacialis* and *P. minutus*.

Contents

Introduction

Understanding and interpretation of the temporal variability of plankton biodiversity in relation to climate and anthropogenic changes is an important field within marine ecology (Planque and Taylor 1998; Beaugrand 2003; Hays et al. 2005). Zooplankton play an important role in marine ecosystems due to their intermediate role in the food web linking primary production to higher trophic levels (Roemmich and McGowan 1995; Richardson 2008). Long-term studies (>10 years) of the biological response of zooplankton to physical variables have yielded valuable information about the forcing of biological dynamics and production in response to environmental variability (Gerten and Adrian 2000; Clark et al. 2001; Perry et al. 2004). But most of these studies are conducted in temporal or Boreal environments (Kane 2007; Conversi et al. 2009; Eloire et al. 2010) as long time series are scare in high-latitude areas.

Inter-annual variations in the dynamics of primary and secondary production is affected by large scale abiotic variability such as climate swings (Gerten and Adrian 2000; Beaugrand et al. 2002; Beaugrand 2003; Orlova et al. 2010). In the northern hemisphere the North Atlantic Oscillation (NAO) accounts for much of this variability as observed in the form of climate fluctuations (Hurrell 1995). Marine zooplankton are good indicators for reflecting the variations in hydrographical and ocean conditions due to their short life-spans and rapid numerical responses to changing environmental variables (Hays et al. 2005). Such responses can affect the plankton biodiversity. For instance in a study of zooplankton samples collected by the Continuous Plankton Recorder survey, Warner and Hays (1994) observed an increase in biodiversity in the North Atlantic Ocean that was linked to a northward movement of relatively warm water masses. This warming was followed by an increase in subtropical taxa (Beaugrand et al. 2002). However, both local and regional shifts in climate (Beaugrand and Ibanez 2004), and local bathymetry (Walkusz et al. 2003) can affect zooplankton communities in confined water bodies such as fjords or inlets, and therefore the dynamics of local species assemblages may not always be directly linked to regional or large-scale physical fluctuations.

Zooplankton studies in Arctic and sub-arctic areas have mostly focused on single key-species, especially the calanoide copepods (Fromentin and Planque 1996; Beaugrand et al. 2002; Taylor et al. 2002; Beaugrand 2003; Beaugrand and Ibanez 2004; Søreide et al. 2010), and often only cover a limited (< 10 years) periods of sampling. In this thesis I have revisited a data set of > 30 years of zooplankton and hydrographical observations. The aim for this

investigation was to take a broader look at the zooplankton community by quantifying seasonal and long-term change in biodiversity and abundance in relation to environmental variability, and to provide new information on how such variability may affect ecological interactions in the zooplankton.

Material and methods

The data sets

The analysis presented here is based on zooplankton and hydrography data from the Chupa Inlet (60° 19.5' N 33° 39.4' E) of Kandalaksha Bay, White Sea, Russia. In total the data set include information from 814 sampling dates between 1963 and 1998. The data set is kindly made available through: (www.nodc.noaa.gov). Sampling was initially conducted every 10^{th} day, but sampling frequency varied particularly in winter after the first years (Table 1) so that data coverage is better in summer months than in winter months. On each sampling date water temperature and salinity was recorded at depths of 0, 5, 15, 25 and 50 m, and near the bottom, 65 m. A deep-water turning-over TG-type thermometer, or a bathythermograph, both with a resolution of 0.1°C where used to measure the temperature. Salinity was measured in water samples obtained by a Nansen water sampler by titration, or by use of an electric salt gauge (GM-65M).

Zooplankton was sampled by a Juday plankton net (area = 0.1 m^{-2}, mesh size = 0.168 mm) fitted with a messenger operated closing device from three standard depth intervals at 10-0, 25-10, and 65-25 m. The plankton sampled was preserved in a 10% formaldehyde solution before enumeration in the lab. 22 species or higher taxonomic groupings are quantified in the data set, here referred to as taxa. The biological diversity in the data set is considerable as both meroplankton and holoplankton are included as well as a variety of different ecologies (Table 2). A more thorough description of the data set may be found in Berger et al. (2001).

Data analysis

To quantify hydrographical variability in the data set the temperature and salinity data were converted in to depth weighted average values and pooled into monthly averages for each year. Based on these monthly averages temperature and salinity anomalies were computed for each year. In addition to these locally obtained variables I used winter NAO

index. This index is derived from the differences in atmospheric pressure between the Azores and Iceland, from December to March (Hurrell 1995) and presented as anomalies. The index was obtained at the website of the Climate Analysis Section within Climate and Global Dynamics Division (CDG) of the NCAR Earth System Laboratory (NESL) (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

Table 1: The distribution over the year of the 814 samples conducted in the Kandalaksha Bay, White Sea from 1963 – 1998.

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
# samples	18	39	39	55	50	96	101	106	107	102	73	28

Frequency occurrences was calculated for each taxa as the percentage of taxa appearance in the data set for each sample, between January 1964 and December 1998. The first quarter (January, February and March = Q1) in 1963, 1972, 1973, 1993, 1994 and 1995 contained little or no data and were therefore excluded from the analysis. In Q2 (April, May, and June), data from 1963 and 1972 are also missing, in Q3 (July, August and September) the data set is complete, and in Q4 (October, November and December) some years are missing data from December.

Also yearly abundance anomalies were obtained by averaging yearly abundances and subtracting them from the average of the entire time series (Fig.1D).A Shapiro-Wilk test was used to test for normality in the zooplankton data. Only three species showed a normal distribution. To test for co-variability between climate related variables (NAO, salinity, temperature) and zooplankton abundances I therefore used Spearman`s correlation test (rho), which does not require normally distributed data.

Taxon specific contribution (%) to the total percentage of zooplankton abundances, in each quarter (Q1 – Q4), was calculated. Each species contribution to the abundance was obtained by dividing the total abundances of each species over the total abundance of every species of the entire year. To detect long-term changes in species abundance linear models was fitted to each species and f-statistic was used to test if a long term trend was present.

Biodiversity was estimated by Shannon`s diversity index using the yearly averaged abundance of all taxa (SHANNON 1948):

$$H' = -\sum_{i=1}^{R} p_i \, log \, p_i$$

Where p_i is the proportion of individuals belonging to the *i*th species. When a few species dominate the overall abundance the Shannon diversity index decreases, while the index increases with a even distributed species composition. To study variability in diversity and species abundances monthly estimates were plotted for all years studied.

A preliminary investigation indicated a biodiversity peak in the months July, August, September and October. Therefore I chose to take a closer look in the taxa co-variability and abundance for these months.

To test for co-variation between the abundance of several taxonomic units and climate variability a multiple regression analysis was performed on all data points from June to October in all years. For this analysis data were Ln+1 transformed to increase evenness of residuals and climate variability (winter NAO, temperature and salinity) were expressed as anomalies. Only significant correlated taxa or climate explanatory variables (Table 4 and appendix Table 1) was used as independent variables. To select the best multiple regression models I used Akaikes information criteria (AIC).

Table 2: Data sets frequency occurrence of zooplankton taxa for the 814 samples included in the data set from the White Sea between 1964 and 1998.

Taxa	**Frequency occurrence (%)**	**Plankton mode**	**Trophic ecology**	**Biogeographic category**
Acartia longiremis	94.84	Holoplankton	Herbivorous – omnivorous	Warmwater
Aglantha digitale	85.87	Holoplankton	Carnivore	Warmwater
Ascidia larvae	9.46	Meroplankton	None feeding	Warmwater
Bivalvia larvae	71.13	Meroplankton	Herbivore	Warmwater
Bryozoa larvae	31.82	Meroplankton	Herbivore	Warmwater
Calanus glacialis	96.56	Holoplankton	Herbivorous – omnivorous	Coldwater

Table 2 continued

Taxa	Frequency occurrence (%)	Plankton mode	Trophic ecology	Biogeographic category
Centropages hamatus	60.07	Holoplankton	Omnivore	Warmwater
Cirripedia naup	44.96	Meroplankton	Herbivore	Coldwater
Echinodermata larvae	35.01	Meroplankton	Herbivore	Warmwater
Fritillaria borealis	83.42	Holoplankton	Herbivore - omnivore	Warmwater
Gastropoda larvae	94.59	Meroplankton	Herbivore	Warmwater
Metridia longa	99.26	Holoplankton	Omnivore	Coldwater
Microsetella norvegica	89.80	Holoplankton	Detritivore / herbivore	Warmwater
Oicopleura vanhoffenis	48.40	Holoplankton	Organic particle	Coldwater
Oithona similis	99.14	Holoplankton	Omnivore - carnivore	Warmwater
Oncaea borealis	98.89	Holoplankton	Carnivore	Coldwater
Parafavella denticulata	38.70	Holoplankton	Herbivore	Warmwater
Podon leuckarti	47.42	Holoplankton	Herbivore	Warmwater
Polychaeta larvae	71.87	Meroplankton	Diatoms	-
Pseudocalanus minutus	100.00	Holoplankton	Omnivore	Coldwater
Sagitta elegans	92.26	Holoplankton	Carnivore	Warmwater
Temora longicornis	71.38	Holoplankton	Omnivore	Warmwater

Results

The total recorded zooplankton abundance ranged from a minimum of 265 ind. m^{-3} in January 1984 to a maximum of 197 815 ind. m^{-3} in June 1989. Similarly, depth averaged temperature and salinity ranged from 1.72 °C in April 1964 to 9.13 °C in September 1967, and from 21.3 psu in October 1994 to 29.62 psu in October 1971.

Yearly anomalies of winter NAO, salinity, temperature, as well as total zooplankton abundance are presented in Fig. 1. Abundance anomalies of the zooplankton data varied between 498 ind. m^{-3} in 1994 and -493 ind. m^{-3} in 1970.

Visual inspection of Fig. 1, suggest that the anomalies of climate indices in the early periods of the data set differ from the late one. Salinity shifts from predominantly negative to positive anomalies from 1979, and a Welch Two Sample t-test confirms that the two periods, prior to 1979 and after 1979, differ ($p < 0.001$). Likewise, temperature and winter NAO both shows predominantly negative anomalies before 1972, fluctuations between positive and negative anomalies in 1972 – 1987, and predominantly positive anomalies thereafter. For both winter NAO and depth averaged temperature there was a significant difference between the

two periods 1963 – 1971 and 1988 – 1998 ($p < 0.001$, and $p < 0.001$, respectively). Before 1980 total zooplankton abundances were characterized by mostly negative anomalies while mostly positive anomalies was observed from 1985 (Fig. 1D).

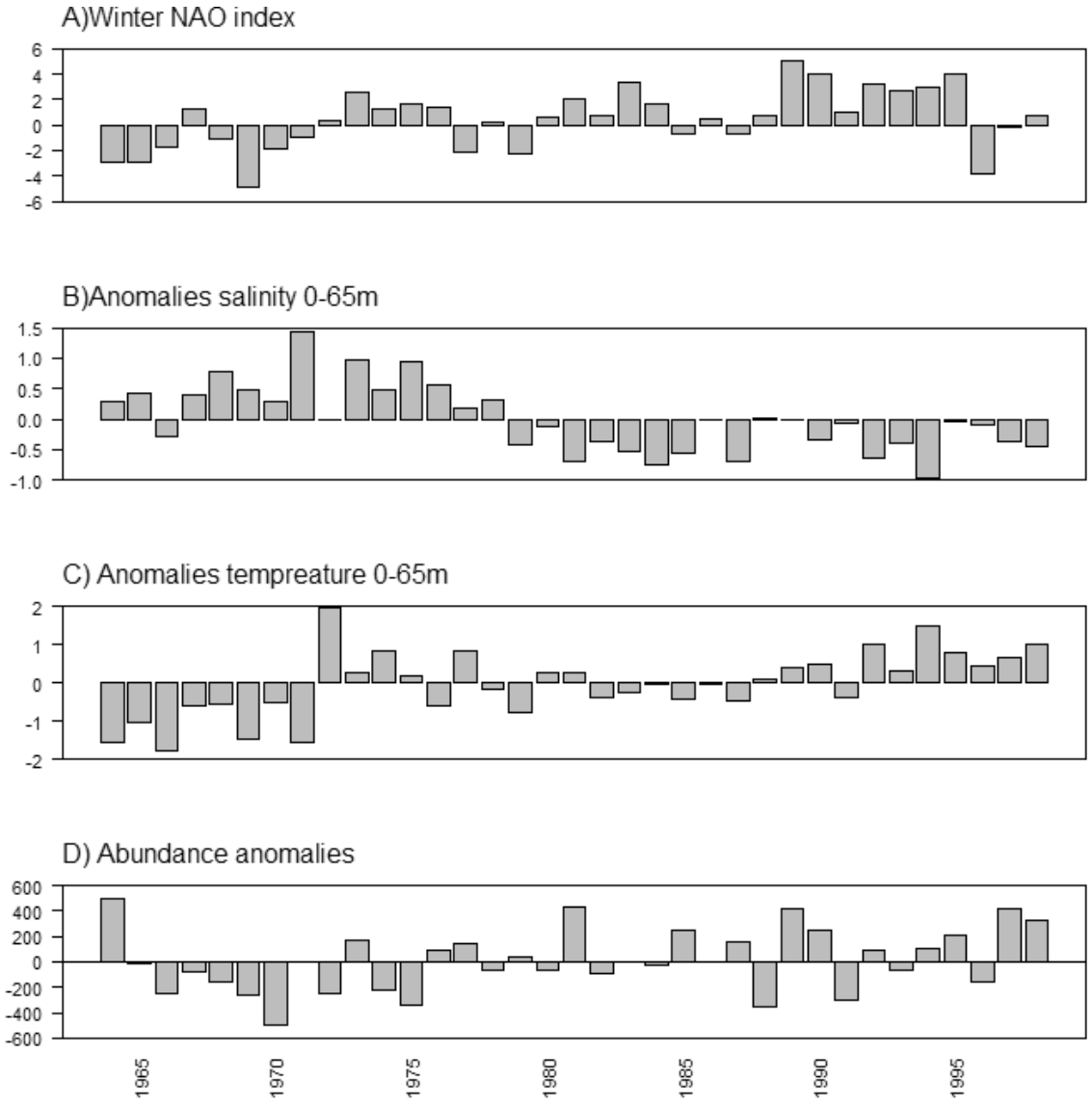

Fig. 1: White Sea temporal variability in environmental and biological data from 1964 to 1998, expressed as (A) winter NAO index, and anomalies of yearly averages for depth averaged salinity (B), temperature (C), as well as (D) total abundance (ind. m^{-3}).

Seasonal variability in species contribution to total zooplankton community

Two species, *O. similis* and *P. minutes*, dominated the samples, and accounted for >70% of total zooplankton abundances in all four quarters (Fig. 2). A group consisting of *A.*

longiremis, *C. glacialis*, *C. hamatus*, *F. borealis*, Gastropoda larva, *M. longa*, *M. norvegica*, *O. borealis* and *T. longicornis* contributed from 14% in Q2 to 24% in Q3. The remaining taxa contributed <1% in Q1 and Q2, and <6% in Q2 and Q3.

Eleven taxa peaked in abundance in the Q3, six peaked in Q2, three taxa peaked in Q1, and two in Q4.

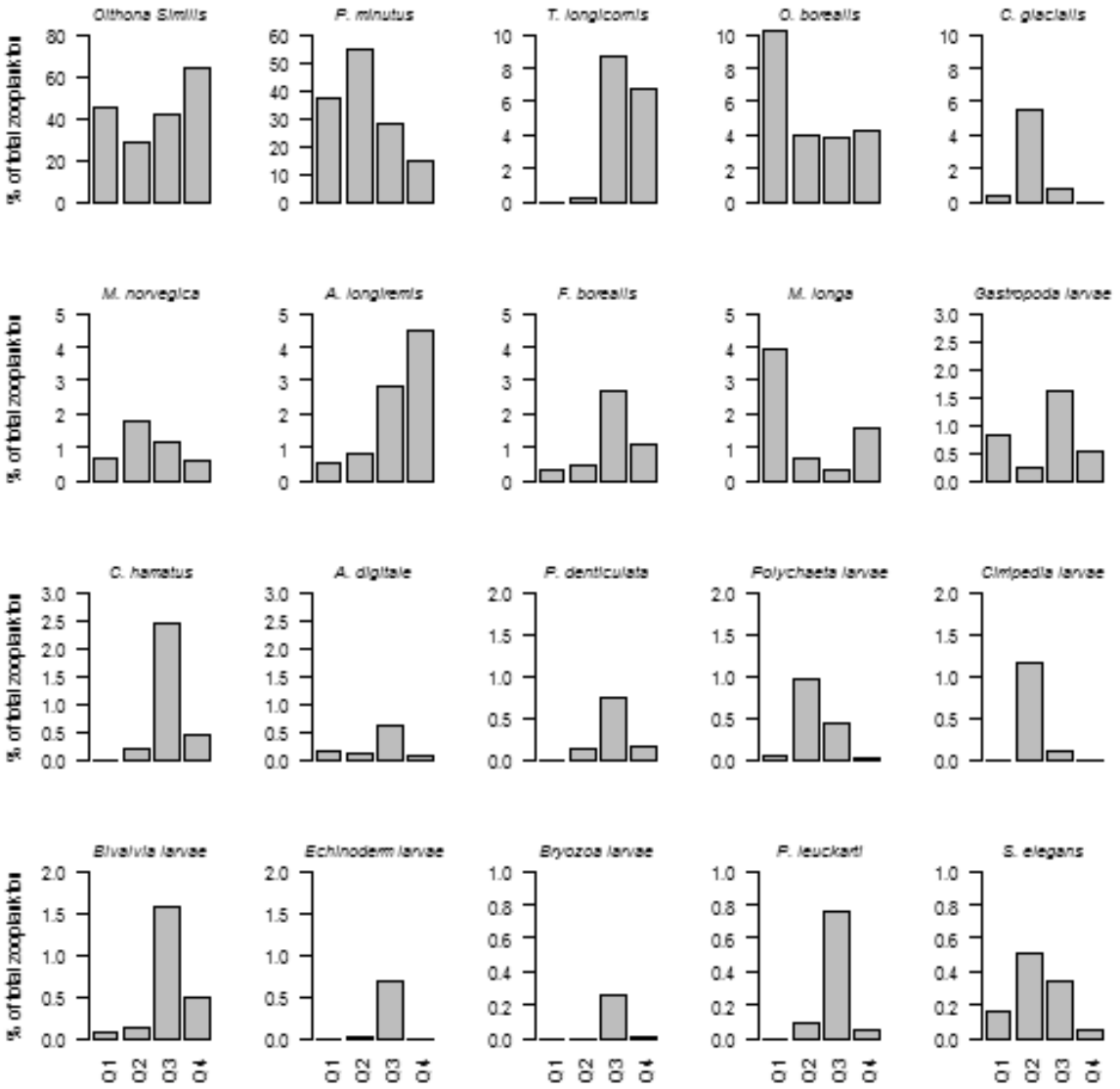

Fig. 2: Seasonal variability in 20 taxa specific contribution (%) to the total abundance by quarters (Q1-4). Note that Y-axes vary between panels.

Temporal trend in species contribution to zooplankton

Species contribution varied substantially (Fig. 3). The two numerically dominating species *O. similis* and *P. minutus* contributed on average over the total study period ca. ≈ 75% of the total zooplankton abundances. *A. longiremis*, *C. glacialis*, *O. borealis* and *T.*

longicornis accounted for ≈ 14% in average of total zooplankton abundance in the sample, while each of the remaining 16 taxa contributed <2%.

Eight taxa showed significant long-term trends in relative contribution to the recorded zooplankton community between 1964 and 1998 (linear regression, $p < 0.05$; Table 4). Five taxa decreased in relative abundance (negative slopes in Table 4: *A. longiremis*, Bivalvia larvae, Echinodermata larvae , *O. similis*, *O. borealis*) *while three taxa (C. glacialis*, *P. minitus* and *S. elegans*) increased in relative abundance.

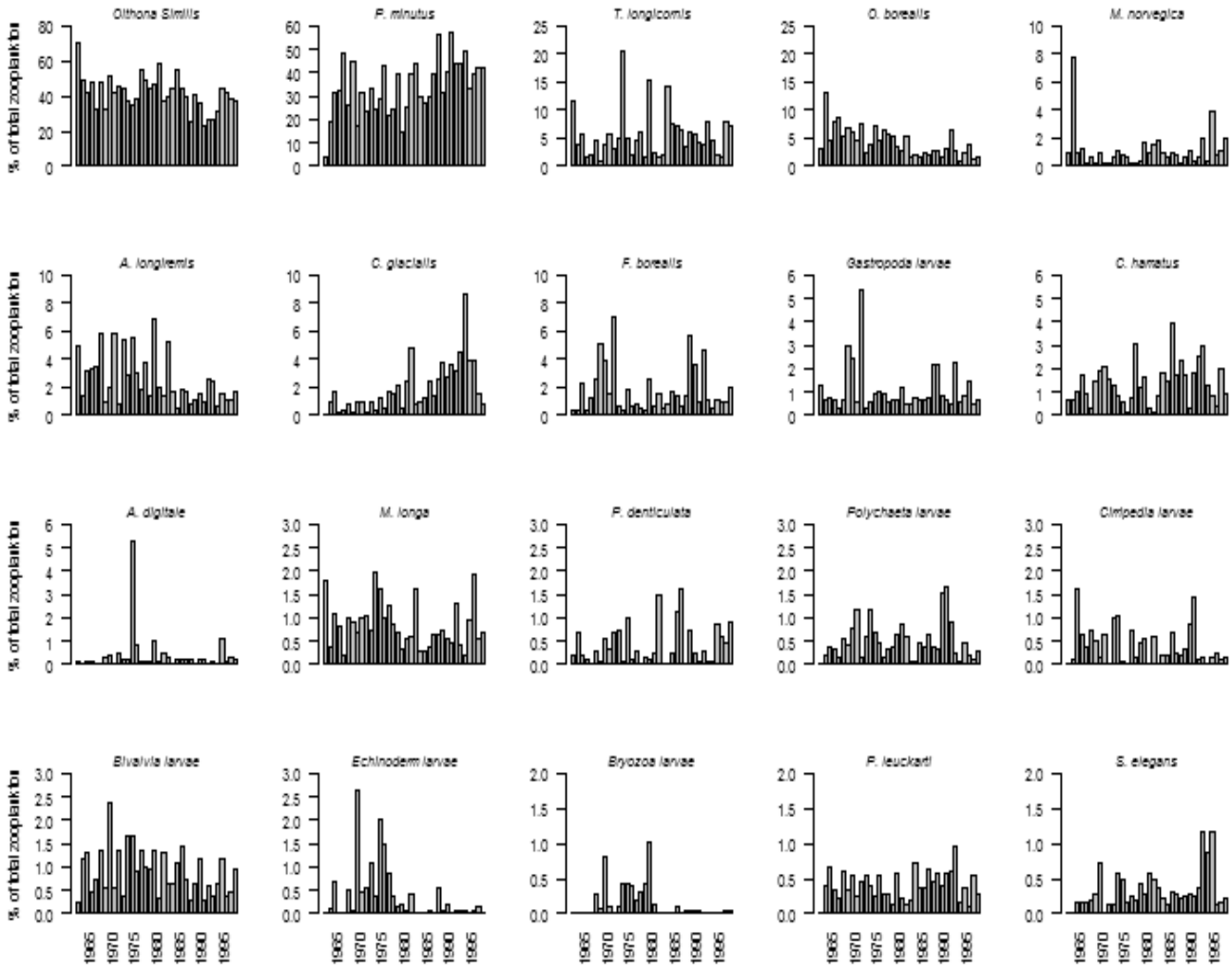

Fig. 3: Temporal variability in contribution as % if yearly averaged abundance to total White Sea zooplankton of 20 taxa included in the data set. Note that Y-axes varies between panels.

Table 3: Significant temporal trends in yearly averaged relative abundance of White Sea zooplankton (detected by linear regression, $p < 0.05$) in the study period 1964 – 1998. Only significant regressions are shown.

Taxa	Slope	Intercept	P value	R^2	DF
A. longiremis	-0.002	4.776	<0.01	0.18	33
Bivalvia larva	-0.001	1.798	<0.05	0.10	33
C. glacialis	0.004	-7.274	<0.01	0.42	33
Echinoderm larva	-0.002	3.360	<0.05	0.11	33
O. Similis	-0.003	6.876	<0.05	0.11	33
O.borealis	-0.004	9.041	<0.01	0.52	33
P. minutus	0.005	-9.520	<0.01	0.19	33
S. elegans	0.001	-1.657	<0.05	0.12	33

Temporal trend in biodiversity

Biodiversity, as estimated by year specific Shannon`s H', remained relatively stable during the decades of sampling (Fig. 4), H´ ranging from 1.34 in 1981 to 1.99 in 1975. Average biodiversity was 1.58. No significant long-term trend was detected by linear regression.

Seasonal distribution of abundances and diversity

The seasonal peak in biodiversity was observed from the start of June to the start of October (Fig. 5A). This roughly overlapped whit the peak in total zooplankton abundance, which lasted from mid May to the end of October. This indicates that the White Sea zooplankton was most diverse and abundant in the months July through October, and in the further analysis I have focused on these months.

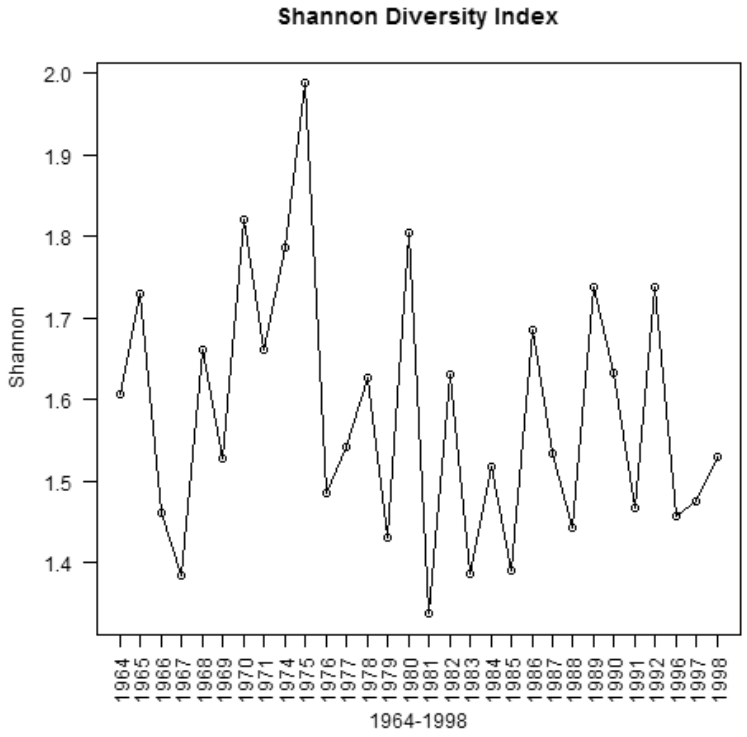

Fig. 4: Yearly biodiversity (Shannon`s H´) in the recorded White Sea zooplankton community data from 1964 – 1998.

Co-variability between climate and zooplankton abundance

Four taxa (*A. digitale*, *O. vanhoffenis*, *O. borealis* and *P. denticulate*) showed signs of co-variation with Winter NAO (Table 4). More than half of the taxa correlated either with temperature and salinity, or with both, and only larval ascidianceans showed no correlation to environmental variables.

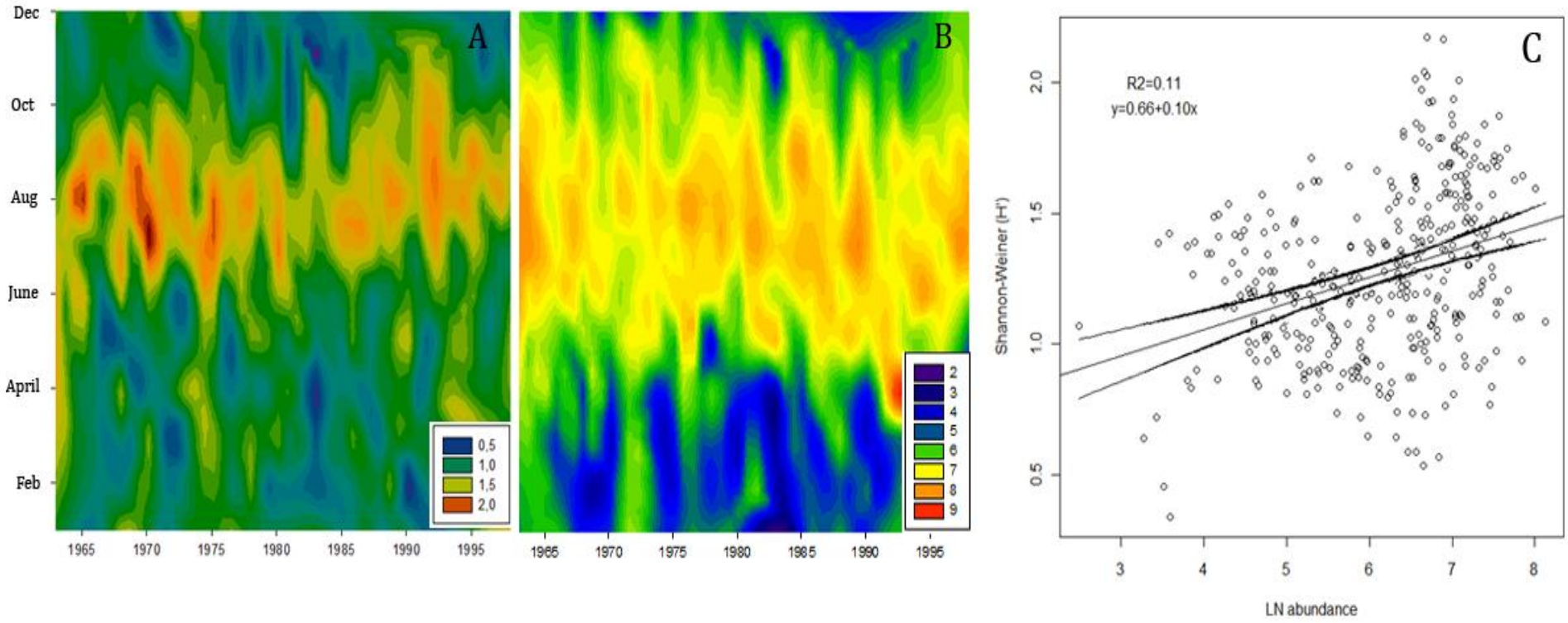

Fig. 5: Seasonal and intra-annual variability in monthly averaged biodiversity expressed as Shannon`s H´ (A) and total abundance (ln-transformed ind. m^{-3}) in the White Sea data set (B). The two are not independent as revealed by the significant linear regression given in the (C).

Table 4: Spearman correlation coefficients (Spearman`s rho) between normalized zooplankton abundance and climate indices. Only significantly (* $p < 0.05$, ** $p < 0.01$) correlations are presented.

Taxa	**Spearman's rho**		
	Winter NAO	**Temperatur e**	**Salinity**
A. longiremis			0.11*
A. digitale	0.10*	0.21**	
Larval ascidiaceans			
Larval bivalves		034**	-0.11*
Larval bryozoans		0.25**	0.17**
C. glacialis			-0.16**
C. hamatus		0.30**	-0.15**
Cirripedia nauplii		0.12*	
Larval echinoderms		0.20**	
F. borealis		0.17**	
Larval gastropods		0.29**	-0.18**
M. longa		-0.23**	0.12*
M,. norvegica		0.13**	-0.14**
O. vanhoffenis	0.21**		-0.12*
O. similis		0.25**	
O. borealis	-0.26**		0.13**
P. denticulate	-013**	0.11*	
P. leuckarti		0.25**	-0.17**
Larval polychaets		0.19**	
P. minutus			-0.23**
S. elegans		0.12*	-020**
T. longicornis		0.31**	

Abundance of 21 out of the 22 taxa included in the data set correlated with one or more of the other taxa (Appendix table 1). The only exception was larval ascidians. *T. longicornis* correlated with seven other species, while the abundance of larval bivalvles and *C. glacialis* both correlated with six other taxa. *P. denticulata* and polychaeta larvae correlated with five and four species, while *M. norvegica*, *O. vanhoffenis* and Cirripedia nauplii all correlated with three species. Bryozoa larvae, *C. hamatus*, Echinodermata laravae,

Gastropida larvae, *M. longa* and *O. similis* covariates with two species. *A. longiremis, A. digitale, F. borealis, P. minitus* and *S. elegans* have all significant ($p < 0.05$) biological interaction with one species.

Multiple regression analysis and model selection

All species had significant ($P < 0.01$) linear regression models (Table 5). The models explanatory level varied from 5 % (larval ascidiaceans) to 68 % (*S. elegans*). In nine species, >50% of the abundance variability could be explained by a multiple regression model. More than half of the models are only consisting of biological interactions. The complexity of the models varied from five (larval ascidiaceans), to eighteen variables (C. *hamatus*). Only biological and environmental data that was significant correlated prior to multiple regression analysis was used.

Discussion

While models were successfully developed for all species or taxonomic groups included in the data set the degree to which models explained variability in abundance varied greatly (as indicated by R^2 values). For six of the 22 taxa < 30% of the variation in abundance could be explained by the fitted multiple regression model. For another seven taxa R^2 was between 0.30 and 0.40, and for the remaining nine taxa R^2 was > 0.5 (Table 5). For three species (*S. elegans, C. glacialis* and *P. minutus*) the models used here explained two thirds of the variability, thus, although simple, the linear regression modeling approach used appear capable of relatively high degree of explanatory value.

Table 5: Taxon-specific models for variability in abundance of 22 taxonomic units as selected by AIC. Taxon in taxonomic unit modeled, Model indicate the multiple linear regression models with environmental and taxonomic variables (NAO = winter North Atlantic Oscilliation index, sal = depth averaged salinity (0-65 m, anomaly), temp = depth averaged temperature (0-65 m, anomaly), A.lon = *A. longiremis*, A.dig = *A. digitale*, Asc = larval ascidiaceans, Biv = larval bivalves, Bry = larval bryozoans, C. gla = *C. glacialis*, C. ham = *C. hamatus*, Cir = cirripedia nauplii, Ech = larval echinoderms, F.bor = *F. borealis*, Gas = larval gastropods, M.lon = *M. longa*, M.nor = *M. norvegica*, O. van = *O. vanhoffenis*, O.sim = *O. similis*, O.bor = *O. borealis*, P.den = *P. denticulata*, P.leu = *P. leuckarti*, Pol = larval polychaets, P.min = *P. minutus*, S.ele = *S. elegans*, T.lon = *T. longicornis*. Abundance data were ln-transformed. All models are significant at 0.99 % level ($p < 0.01$).

Taxon	Model	R^2	AIC
A. longiremis	0.27+0.06*Bry-0.17*C.gla+0.10*C.ham+0.10*M.nor+0.44*O.sim+0.26*O.bor-0.04*P.den+0.10*Pol-0.17*S.ele+0.02*sal	0.31	189.3
A. digitale	2.10+0.14* Bry -0.08*C.gla+0.06* C.ham -0.06*Cir+0.12* Gas -0.21* P.min +0.66* S.ele +0.04*NAO	0.41	207.9
Larval ascidiaceans	0.52-0.04*Cir-0.07* P.min +0.06*T.lon	0.05	-207.3
Larval bivalves	0.34+0.10* Bry -0.10* C.gla +0.09* Cir +0.06* Ech +0.32* Gas +0.09*M.nor+0.21*O.sim+0.08* P.leu +0.06*Pol+0.09* S.ele -0.02*sal+0.10*temp	0.51	139.6
Larval bryozoans	-0.94+0.22* A.lon +0.08*A.dig+0.11*Biv+0.31* Ech -0.14* O.sim +0.17* T.lon +0.03*sal+0.07*temp	0.29	405.3
C. glacialis	-5.85-0.20*A.lon-0.10* Biv +0.08* C.ham +0.08* M.nor +0.25* O.bor +-0.05*P.den+0.10* P.leu +0.15* Pol +1.05* P.min -0.10* T.lon	0.67	87.5
C. hamatus	-1.22+0.22* A.lon -0.16* Biv +0.18* C.gla +0.14* Cir +0.18* Gas -0.23* M.lon -0.23* O.van -0.19* O.sim +0.07* P.den +0.10* P.leu +0.29* P.min +0.56* T.lon +0.08*temp	0.49	384.4
Cirripedia nauplii	-1.73-0.17* Asc +0.08* Biv +0.08* C.ham +0.24* Ech +0.13*F.bor+0.14* O.sim -0.20* O.bor +0.06* P.den +0.09* P.leu +0.21* P.min -0.12* T.lon	0.44	224.4
Larval echinoderms	-0.19+0.18* Biv +0.30* Bry +0.33* Cir +0.18* Gas +0.33* Pol -0.23* T.lon	0.56	366.7
F. borealis	6.10+0.14* Biv +0.35* Cir +0.30* Gas -0.16* M.lon +0.12* P.den -0.48* P.min	0.21	630.9
Larval gastropods	-1.42+0.07* A.dig +0.26* Biv +0.09* C.ham -0.06* Ech +0.07* F.bor -0.06* M.nor -0.12* O.van +0.18* O.sim +0.10* O.bor +0.12* P.leu +0.17* P.min +0.09* S.ele	0.53	79.3
M. longa	3.10-0.08* C.gla -0.11* C.ham -0.05* F.bor +0.16* O.van -0.08* P.leu +0.27* P.min -0.13* S.ele -0.08*temp	0.16	215.6
M.. norvegica	-0.20+0.16* A.lon +0.11* Biv +0.21* C.gla -0.07* C.ham +0.14* O.sim +0.21* P.den +0.12*P.leu+0.09* P.leu +0.03*sal	0.35	396.1
O. vanhoffenis	-0.83-0.06* A.lon -0.08* C.ham +0.07* M.lon +0.18* O.sim -0.16* O.bor -0.04* P.den +0.15* P.min	0.10	-129.9
O. similis	4.43+0.19* A.lon -0.06* C.ham +0.05* Cir +0.08* Gas +0.05* M.nor +0.22* O.bor +0.06* P.den -0.04* P.leu +0.10* S.ele +0.20* T.lon	0.42	-187.4
O. borealis	2.19+0.12* A.lon +0.06* Biv +0.17* C.gla -0.10* Cir +0.06* Ech +0.06*Gas-0.13* O.van +0.26* O.sim -0.07* P.leu +0.11* P.min -0.08* T.lon -0.08*NAO	0.38	-112.3
P. denticulate	-5.89-0.15* A.lon -0.19* C.gla +0.22* Cir +0.10* Ech +0.12* F.bor +0.35*M.nor-0.20*O.van+0.44* O.sim +0.46* P.min -0.13* S.ele	0.26	632.2
P. leuckarti	-0.03+0.20* A.lon +0.19* Asc +0.15* Biv +0.11* Bry +0.21* C.gla +0.16* C.ham +0.15* Cir +0.29* Gas -0.13* M.lon +0.12* M.nor -0.14* O.sim -0.25* O.bor +0.11* Pol +0.23* S.ele	0.55	386.5
Larval polychaets	0.01-0.14* Asc +0.12* Biv +0.27* C.gla +0.29* Ech +0.10* M.nor +0.09* P.leu +0.11* S.ele -0.07* T.lon +0.10*temp	0.53	311.1
P. minutus	6.00-0.04* A.dig +0.26* C.gla +0.04* C.ham +0.03* Cir -0.03* Ech -0.02* F.bor +0.06* Gas +0.05*M.lon+0.03* M.nor +0.05* O.bor +0.03* P.den +0.18* S.ele	0.66	-446.0
S. elegans	-2.66-0.17* A.lon +0.38* A.dig -0.12*Asc+0.08* Biv +0.06*Gas+0.17* O.sim -0.04* P.den +0.11*P.leu+0.05* Pol +0.53*P.min-0.23* T.lon +0.02*sal	0.68	-20.4
T. longicornis	2.12+0.12*Asc+0.08*Bry-0.16* C.gla +0.04*C.ham-0.08* Cir -0.14*Ech+0.04* F.bor +0.58* O.sim -0.23*O.bor-0.27*S.ele+0.14*temp	0.54	256.7

It is perhaps more surprising that while all the selected models included information on the abundance of other taxonomic units only half of them contained information on climate variability (temperature, salinity, NAO). Thus, my results indicate that effects of biological variability, overall, may be stronger driver for the variability, and thus biodiversity, in Arctic zooplankton community that the more climate related variability indices such as NAO and hydrographical anomalies. The majority of studies on zooplankton ecology have revolved around single zooplankton species (Reid et al. 1998; Daase and Eiane 2007; Søreide et al. 2010), and it is possible that important biological links have been neglected due to a narrow choice of study. However, as my statistical models are relatively crude (i.e. linear regression models without interactions between variables) further research into this matter must be conducted before conclusions can be drawn.

An alternative interpretation could be that biological variability in the data set is driven by climate variability, thus climate variability could be the main driver, but comes out in models as indirect effects through biodiversity. As the climate indices in the present study are fairly coarse, (i.e. anomalies of depth integrated temperature and salinity) and regional responses to other types of climate related variability filtered through biodiversity effects and represented as interactions and co-variability in the community. The requirements for such an interpretation to hold is that such climate related variability do not correlate strongly with water column salinity, temperature and winter NAO. Unfortunately the data set used does not contain information to test for the importance of other climate related drivers.

The links of co-variability between the studied 22 taxa and temperature, salinity, and winter NAO of the models in Table 5 are presented in Fig. 6. While it remains unclear to what extent this pattern of co-variability reflects ecological processes such as predator-prey, or competitive interactions, it could be seen as a first expression of the biocomplexity underlying ecosystem functioning in Arctic zooplankton communities. Note that this representation is severely limited as it does not include the many links to most microorganisms and macro predators likely to be of high importance for the ecosystem.

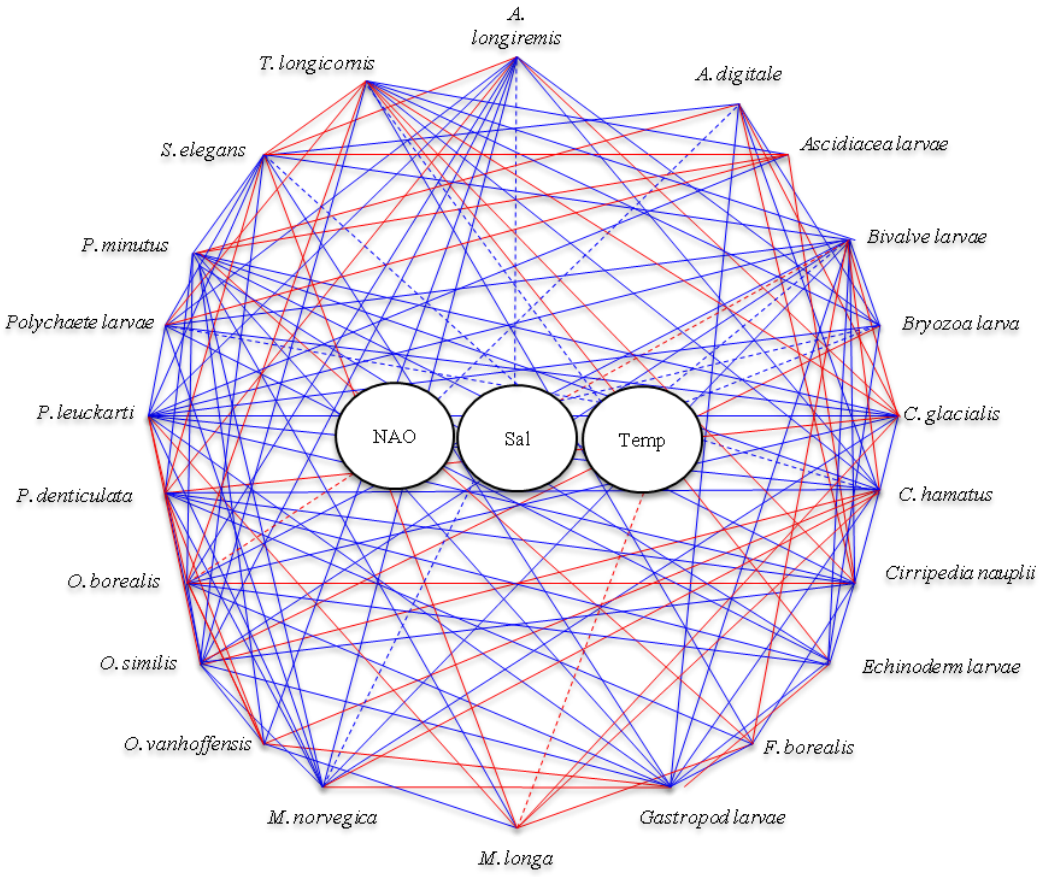

Fig.6: Complexity in the White Sea zooplankton represented by statistically modeled co-variability between the relative abundance of the 22 taxonomic units studied and climate related indices (winter NAO index, White Sea anomalies in salinity (Sal) and temperature (Temp)) for the period 1963 – 1998. Blue lines indicate positive co-variability slopes in modeled co-variability, red lines indicate negative slopes, full lines are co-variability between two taxonomic units, and broken lines represent co-variability between a taxonomic unit and a physical climate index. The figure is based on the AIC selected models presented in Table 5.

The number of co-variability links affecting each taxa in the above representation of biocomplexity likely addresses the strength of that taxon's contribution to to the regulation of biodiversity in the community (Paine 1966). If this holds true for the analysis presented here it is suggested that the dynamics of larval bivalves (16 links), *C. hamatus* (15), *P. minutes*, *O. borealis* (14) have a stronger impact on biodiversity than *M. longa*, *A. digitale* (8 links), *F. borealis* (7), and larval ascidiaceans (6). Although speculative at this point, this interpretation of the results presented in this thesis provides a starting point for disentangling the relationship between biodiversity, biocomplexity and ecosystem functioning in zooplankton communities.

Seasonal variability in zooplankton

Zooplankton biomass and biodiversity peaked in Q2 and Q3 (Fig. 2).This is coherent with reports from other similar locations (Weslawski et al. 1988; Eloire et al. 2010). However, my analysis of abundance (Fig. 5B) does not have fine enough resolution to detect the two peaks in abundance per year often reported in such study (Eloire et al. 2010), but in an analysis of the same data set as I have used (Berger et al. 2001) concludes that Arctic zooplankton reach abundance peaks both in spring and autumn. They also states that Arctic-boreal species reaches maximum abundance in spring and in the beginning of the summer, and the abundance of boreal species peak in the late summer. This is coherent with findings presented in this thesis (Fig. 5A) where biodiversity peaked in Q3, and remained low during the winter months. This deviates from the situation in the northern California current system where high diversity in winter is linked to an inflow of sub-tropical water (Hoff and Peterson 2006). The advection of water in to the White Sea is severely limited due to geographical separation from the Barents Sea (Berger et al. 2001), and this study shows that there is a positive correlation between species abundance and biodiversity (Fig 5C). Cold winter months is replaced by a rapid warming of water in the spring, giving the plankton community favorable conditions for feeding and reproductions, resulting in that zooplankton species reach their maximum abundance from spring to autumn (Søreide et al. 2010) .

Precipitation varies between years, and the salinity is lower in the White Sea than in the Barents Sea due to limited exchange with the Barents Sea, and fresh water inflows from rivers (Berger et al. 2001). This variation is a common feature of similar Arctic and subarctic fjords ecosystems (Weslawski et al. 1988; Renaud et al. 2007). The White Sea is ice covered approximately half of the year, but the sea ice conditions could vary between years, causing differences in the zooplankton development (Berger et al. 2001).

Intra-annual variability in diversity

Co-variation analysis indicates that temperature and salinity are the environmental factors that explain variability in taxa abundance during the months that showed highest biodiversity. The winter NAO index is significant correlated with four taxa, while temperature is significant with sixteen taxa. Since the NAO influences the temperature, one could estimate that the two environmental factors would be closely linked to each other (Hurrell 1995). However, it seems like the winter NAO does not influence the abundance of the months that

have highest biodiversity, and that the temperature present at that time is more closely linked to the abundance variation. It could be argued that the response of the taxa to winter NAO are possible present in the data set, but my choice of zooplankton study period, are not directly related to the winter temperatures, but it is commonly known that the winter NAO might affect the variability in long-term changes of zooplankton abundance and seasonal timing (Planque and Taylor 1998; Reid et al. 1998; Beaugrand 2003; Hays et al. 2005). In taxa that covariates both with temperature and salinity it is indication of that a positive co-variation with temperature gives a negative co-variation with salinity. The only taxa (Ascidians) that had no co-variation with environmental variables are the least abundant taxa in the data set (Table 2).

It is widely accepted that multiple factors , such as ice cover, light conditions and stratification are some of the hydrographical conditions that influences the onset of spring bloom (Francisco Rey et al. 2000; Svendsen et al. 2002; Barange et al. 2010; Søreide et al. 2010), and that they are closely linked to the atmospheric circulation system (Hurrell 1995). The seasonal variation in taxa specific contribution in the White Sea could, however, also be partly due to differences in life cycle strategies among taxa, For instance, (Beaugrand et al. 2002; Hoff and Peterson 2006) defines *C glacialis*, *P minutus* and *O. borealis* as Arctic species that reach their maximum abundance in the spring while the more warm water associated species, such as *T. longicornis* and *C. hamatus*, tend to peak in abundance in August (Berger et al. 2001). The influences of an earlier ice break on herbivore species, such as C. glacialis, are not known, but Søreide et al. (2010) argues that a mismatch between primary production and the Arctic grazers would have a direct effect on higher trophic levels due to a change in the lipid-driven Arctic marine ecosystem, and a species shift from Arctic lipid-rich grazers to temperate and less lipid-rich organisms could be a consequence (Falk-Petersen et al. 2007).

The density of the two most abundant taxa, *O. similis* and *P. minutus* in the study area showed opposite trends in abundance from the mid eighties onwards. The total contribution to the zooplankton community of the small omnivore copepod *O. similis* declined, while the filter feeding *P. minutus* increased, suggest that the zooplankton community shifted from feeding on small zooplankton to phytoplankton (Walkusz et al. 2003). At the same time the relative abundance of the less numerous species the polar herbivore *C. glacialis* (Fleminger

and Hulsemann 1977) and the carnivore *S. elegans* (Feigenbaum 1982) increased. Feigenbaum (1982) found in his lab experiment that digestion time of *S. elegans* is temperature dependent, and that in a 0°C environment it takes *S. elegans* almost three times longer to digest food, than in a 15 °C. Thus a warming of the White Sea could increase *S. elegans* predation efficiency (by reducing prey handling time) thereby increasing growth rate and abundance. There is also evidence of a long-term change in seasonal variability of the species that have their abundance peak in the second quarter. Out of the six species, three (*P. minutus*, *C. glacialis* and *S. elegans*) showed a significant positive long-term trend in their yearly contribution to the total Zooplankton abundances (Table 3).

Concurrent with the temperature anomalies suggesting a warming in Kandalaksha Bay, total zooplankton went from predominately negative anomalies to positive anomalies from the mid eighties onwards (Fig. 1). This increase in zooplankton abundance is coherent with findings from other long-term zooplankton studies form similar periods (Pershing et al. 2005; Kane 2007). However, my result also indicate an increase in the contribution of the Arctic species *C. glacialis* and *P. minutus* and a decrease in the warm water associated species *A. longiremus* and *O. similis* (Fig. 3 & Table 3). In the eastern North Atlantic Ocean, zooplankton has experienced a northward extension of warm water species of more than 10° latitude that are associated with an concurrent decrease in coldwater species, v but in the western Labrador Sea Arctic species has increased (Beaugrand et al. 2002). Renaud et al. (2007) suggested in his study of the benthic community structure, in van Mijenfjord, that fjords with a sill may be less influenced of the northward movement of species, and that the local environmental regimes (freshwater runoff, ice conditions and local circulation patterns) are more important to the ecosystem species composition than the large scale climate variability pattern.

Conclusion

Changes in plankton community diversity may reflect modifications in the hydrographical environment (Beaugrand et al. 2002; Hays et al. 2005). The work presented here indicates that multiple co-variability occurred between abundance of all studied species or other taxonomic units and with climate related environmental variability. This suggests that biodiversity as an ecological variable also provide information regarding climate change, and supports the view that biodiversity may act as a rather sensitive measurement of changes over

time (Taylor et al. 2002). The northward trend in the distribution of zooplankton and the large-scale changes in ecosystem species composition detected throughout much of the Northern Atlantic Ocean (Beaugrand et al. 2002) was not detected in the White Sea, and seems to suggest that semi-closed fjords respond to large-scale hydro climatic processes different from more open coastal systems (Renaud et al. 2007).

The results of the present work indicates that in order to understand the complexity of the marine plankton ecosystem response to fluctuating physical variables it is necessary to invest time in studying the ecological interactions in plankton communities, as biodiversity, and not only species composition in relation to physical impacts. Evidence of change is present even in ecosystems that are not greatly influenced by water exchange.

Mantua (2004) recommends analyzing biological and physical data separately, to identify and isolate ecosystem behaviors from other influences like environmental change. This thesis suggests that ecological effects of climate variability depend not only on changes in the physical environment, but to an even larger extent co-vary with biodiversity in ways that may signify species interactions.

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Appendix

Table 1. Biological co variability between taxa. Only significant ($p < 0.05$ *, $p < 0.01$ **) co variability is showed. 1: *A. longiremis, 2: A.digitale, 3:* Ascidia larvae, 4: Bivalvia larvae 5: Bryozoa larvae *6: C. glacialis 7: C. hamatus* 8: Cirripedia larvae 9: Echinoderm larvae *10: F. borealis* 11: Gastropoda larvae *12: M. longa 13: M. norvegica 14:O. vanhoffenis 15: O. Similis 16: O. borealis 17:P. denticulata 18:P. leuckarti* 19:Polychaeta larvae *20: P. minutus 21: S. elegans.*

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
Larval bivalves	**	**	-*																		
Larval bryozoans	**	**		**																	
Calanus glacialis	-*	**	-**	**																	
C. hamatus	**	**		**	**	**															
Cirripedia nauplii		**	-**	**	**	**	**														
Larval echinoderms		**	-**	**	**	**	**	**													
Fritillaria borealis		**		**	**	*	**	**	**												
Larval gastropods		**	-**	**	**	**	**	**	**	**											
Metridia longa		**		-**	-*	-**	-**	-**	-**	-**	-**										
Microcetella. norvegica	**	**	-**	**	*	**	**	**	**	**	**	-*									
Oikopleura vanhoffenis	-**						-**				-**	**									
Oithona similis	**	*		**	**		**	**	**	**	**		**								
O. borealis	**	**	-**	**		**	**	**	**		**		**	-**	**						
P. denticulate	*	**		**	**	**	**	**	**	**	**		**	-*	**	**					
P. leuckarti	**	**	-*	**	**	**	**	**	**	**	**	-**	**		**	**	**				
Larval polychaets		**	-**	**	*	**	**	**	**	**	**	-**	**		**	**	**	**			
P. minutus		**	-**	**		**	**	**	**	*	**	-**	**		**	**	**	**	**		
S. elegans	-**	**	-**	**		**	**	**	**	**	**	-**	**	*	**	**	**	**	**	**	
T. longicornis	**		**		**	-**	**	-**	-**					-**	**	**	**		-**	**	-**